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Short Communication

Invertebrate-biased diet of burrowing owls in a newly-restored coastal grassland

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Abstract

Recovering biodiversity across trophic levels is a major challenge in restoration ecology. Specifically, predator population recovery depends on the timely re-establishment of their preferred prey species in restored habitats. Here, we evaluate potential dietary factors contributing to the loss of western burrowing owls (*Athene cunicularia hypugaea* (Bonaparte, 1825)) from a newly-restored coastal grassland. We examined owl pellets and found that burrowing owl diets were relatively low in vertebrate prey during their brief occupation of the restoration site (2.6% of prey items; found in 61.8% of sampled pellets). We suggest that preferred food limitation may have been one contributor to the loss of owls from the restoration site. These findings suggest the need to prioritise re-establishment of prey communities for effective long-term recovery of burrowing owls in restored landscapes.

Key words: *Athene cunicularia*, burrowing owl, food web, raptor, restoration ecology, rodent

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Introduction

Grassland ecosystems have undergone severe degradation due to human activity and are among the most threatened ecosystems globally (Samson and Knopf 1994; Gang et al. 2014; Bardgett et al. 2021). Habitat restoration is one of the principal tools for recovering grassland biodiversity and ecosystem services (Martin et al. 2005; Déri et al. 2011; Török et al. 2021). Because restoration efforts often employ a bottom-up approach focused on re-establishing native plant communities, a major ongoing challenge is supporting higher trophic levels in restored grasslands (Serrouya et al. 2011; Fraser et al. 2015). As such, monitoring ecosystem functionality in terms of trophic interactions is crucial for holistically assessing the success of restoration efforts (Martin et al. 2005; Wortley et al. 2013; Vander Zanden et al. 2016)

In California, where grasslands have undergone large-scale degradation (Hamilton et al. 2002), restoration has been emphasised as a tool for providing foraging habitat for threatened raptor populations, with variable success (Woodbridge 1998; Watson 2018; Wolf et al. 2018). In particular, the success of these interventions depends on the concomitant re-establishment of prey

communities (Wolf et al. 2018). Western burrowing owls (*Athene cunicularia hypugaea* (Bonaparte, 1825)) are widely distributed dietary generalists that subsist on a broad range of arthropod and vertebrate prey (Martin 1973). Once considered common throughout California, burrowing owls have declined across the State, with the most severe declines occurring in coastal grasslands (Dawson 1923; Martin 1973; DeSante et al. 2003; Kidd et al. 2003; Sauer et al. 2022; Center for Biological Diversity 2024). The species is now classified as a Species of Special Concern (Shuford and Gardali 2008) and was recently petitioned to be listed as Endangered or Threatened under the California Endangered Species Act (Center for Biological Diversity 2024). Grassland restoration could help mitigate habitat loss for burrowing owls, provided that their associated prey communities can be successfully re-established.

Here, we present a case study of the diet of a small burrowing owl population occupying a newly-restored coastal California grassland. Following initial restoration efforts, wintering burrowing owls temporarily colonised the restoration site, but did not persist at the site. We evaluate the diet of burrowing owls during their occupancy of the restoration site, in particular, assessing their relative intake of vertebrate prey (e.g. rodents), which may be limited in young restoration sites (Patten 1997; Wolf et al. 2018). In doing so, we provide insights into potential challenges faced by burrowing owls foraging in newly-restored grasslands.

Methods

Restoration site and burrowing owl population

We surveyed the diet of burrowing owls nesting at the North Campus Open Space (NCOS) restoration site on the University of California, Santa Barbara campus in Goleta, California (34.419758, -119.875793); (Cheadle Center 2016). NCOS represents 0.5 km^2 of upland and wetland habitats restored from the site's previous conversion to the Ocean Meadows golf course in the 1960s. Restoration of the site began in 2017 and is ongoing. This restoration site is characterised by grasslands, coastal sage scrub and salt marsh habitat bordered by eucalyptus windrows. After initial site grading, approximately 60 refuge features were created by partially filling 1-metre-deep holes with off-set concrete slabs, with the intention of providing refugia for small mammals, birds and reptiles. In 2020, six additional artificial burrows with longer passageways and an inner chamber were installed specifically to support burrowing owls.

Pellet collection, dissection and morphological identification of faunal remains

To assess burrowing owl diet composition, we collected 34 pellets from three artificial burrows between September 2020 and April 2021. To prevent disturbance, we collected pellets no more than once per week and only when owls were not present. After collection, we stored pellets at -20 °C until dissection.

We followed standard protocols for owl pellet dissection (Lyman et al. 2003; Moulton et al. 2006; Chandler et al. 2016) and identified faunal remains to order, genus or species where possible. Rodent identifications were performed

by Paul W. Collins (Curator Emeritus of Vertebrate Zoology, Santa Barbara Museum of Natural History) and invertebrate identifications were performed by Katja C. Seltmann (Cheadle Center for Biodiversity and Ecological Restoration, University of California, Santa Barbara). We counted individuals in each pellet as the minimum possible number of individuals inferred from anatomical fragments (e.g. two rodent femurs found in one pellet would be scored as a single rodent; two earwig cerci would be scored as a single earwig). For each prey category, we calculated the frequency of occurrence in pellets as the percentage of pellets containing at least one individual of that prey category. To estimate biomass of each prey category, we sourced body mass values from literature, inferring at the genus level and averaging across sexes where necessary (Gettinger 1984; Thompson 1985; Velarde et al. 2007; Hodson et al. 2011; Kovac and Stabentheiner 2012; Ball et al. 2015; Lefebvre et al. 2019). For the unidentified *Rodentia*, we assumed mass was equal to that of the most common rodent sample in our study (*Reithrodontyomys megalotis* Baird, 1857). Likewise, for the unidentified Coleoptera, we assumed mass was equal to that of the most common beetle genus in our study (*Calanthus* sp. Bonelli, 1810). All pellets and contents were deposited in the UCSB Vertebrate Zoology Collection (see Suppl. material 1 for accession numbers).

Results

Between winter 2018–19 and winter 2020–21, three burrowing owls were observed overwintering in the artificial burrows at NCOS. No breeding behaviour was observed, as no owls persisted at the site into the breeding season. Across the 34 pellets sampled from this small population, we identified a total of 1533 prey individuals (Table 1). Pellets contained on average 45.1 individuals per pellet (std. error = 6.1). Every pellet contained invertebrates (all arthropods), which represented 97.4% of prey by number and 22.8% by biomass (inferred from literature estimates). Remains of orthopterans (Gryllidae and Caelifera) were identified in 22 pellets, but no body parts were sufficiently recognisable to reliably count and so are excluded from these estimates. Twenty-one pellets contained vertebrate prey (2.6% by number, 77.2% by biomass), all of which were rodents.

Discussion

In this study, we provide evidence that an ephemeral burrowing owl population subsisted primarily on arthropods during its brief occupancy of a newly-restored grassland. In Santa Barbara County, CA, where burrowing owls have been nearly extirpated (Lehman 1994), grassland restoration is a crucial first step in efforts to conserve threatened raptors. However, small mammal populations may not immediately or reliably re-occupy restored grasslands (Wolf et al. 2018), limiting food opportunities for predatory species. Given the local precarity of burrowing owls, our focal population was small and transient, limiting our pellet sample size and the generalisability of our findings. However, samples like these that capture temporary occupancy by locally rare species can provide valuable insights into the ecological factors driving local population declines.

Table 1. Prey items represented as the total number of individuals found across all 34 pellets (*n*), the percent of the total number of prey items across all pellets, the frequency of occurrence (percentage of pellets containing at least one of a given taxonomic group) and the total estimated biomass across all samples.

Prey Item	Common Name	*n*	% of prey items	% freq.	Estimated Biomass (g)
Forficula auricularia Linnaeus, 1758	European earwig	728	47.5	94.1	55.3
Coleoptera	Beetles	394	25.7	82.3	43.3
Armadillidium sp. Brandt, 1831	Woodlouse	331	21.5	32.3	32.4
Vespula pennsylvanica (de Saussure, 1857)	Western yellowjacket	40	0.2	11.8	3.0
Reithrodontyomys megalotis Baird, 1857	Western harvest mouse	24	1.6	29.4	208.7
Unidentified *Rodentia* sp.	Rodent	10	0.6	20.6	87.0
Mus musculus Linnaeus, 1758	House mouse	5	0.3	8.8	53
Thomomys bottae Eydoux & Gervais, 1836	Botta's pocket gopher	1	0.1	2.9	103.8
Orthoptera	Grasshoppers, locusts, crickets	NA	NA	64.7	NA

Prey species identified in our sample were consistent with known burrowing owl diet preferences (Coulombe 1971; Barrows 1989; Littles et al. 2007; MacCracken et al. 2021; Gonzalez Rojas et al. 2022). Pellet contents were dominated by European earwigs (*Forficula auricularia* Linnaeus, 1758); (as in Coulombe 1971), which tend to associate with owl burrows and which were identified in all but two pellets. The western harvest mouse (*Reithrodontyomys megalotis* Baird, 1857) was the most common vertebrate prey species, identified in nearly a third of pellets. The one notable exception to known burrowing owl prey in our sample was the western yellowjacket [*Vespula pennsylvanica* (de Saussure, 1857)], found in four pellets, with one pellet consisting entirely of 28 yellowjackets. Some birds are known to prey on stinging social wasps (Birkhead 1974; Raw 1997), though, to our knowledge, this behaviour has not been reported for burrowing owls. Repeated consumption of aggressive, venomous prey is another possible indicator that preferred prey may be limiting at the restoration site.

The relative abundance of invertebrates in burrowing owl pellets is highly variable across seasons and habitats (Table 2). In our study, invertebrates represented 97.4% of prey items by number, placing it at the upper end of known values from published burrowing owl pellet data (mean = 82.1% invertebrates, range = 55–98%); (Marti 1974; Schlatter et al. 1980; Thompson and Anderson 1988; Barrows 1989; Schmutz et al. 1991; Plumpton and Lutz 1993; Moulton et al. 2006; Littles et al. 2007; Nabte et al. 2008; Mrykalo et al. 2009; Trulio and Higgins 2012; Gonzalez Rojas et al. 2022); (Table 2). Notably, invertebrates were identified in all pellets, in contrast to previous studies that identified invertebrates in fewer than two-thirds of pellets (Thomsen 1971; Tyler 1983; Barrows 1989; Mills 2016; MacCracken et al. 2021). Importantly, our invertebrate frequency and biomass estimates are underestimates, due to our exclusion of orthopterans, which we were unable to reliably count, but which were found in two-thirds of pellets.

Because burrowing owl diet composition is thought to be strongly related to prey availability (Errington and Bennett 1935; Barrows 1989; Plumpton and Lutz 1993), the low proportion of vertebrate prey in pellets suggests low rodent abundance and/or strong competition for rodent prey at the restoration site. This possibility is supported by small mammal survey data from the site (Rickard 2023). The live-trap capture rate of rodents in in spring 2021, the time of our study, was 0.04 individuals per trap per night (4% trapping success). Survey data from an adjacent natural reserve site (Coal Oil Point Reserve, 34.408212, -119.877952)

Table 2. Relative proportion of invertebrates in burrowing owl diets characterised in previous pellet analyses. Only studies reporting absolute frequencies of prey items are included. Where multiple years or sampling sites were reported in a single study, we report the mean value.

Reference	Sampling time	Study location	% Invertebrates (by number)	% Invertebrates (by mass)
Present study	Fall 2020–spring 2021	Santa Barbara Co., CA, USA	97.4	22.8
Marti (1974)	Year-round, 1966–1970	Larimer Co., CO, USA	90	NA
Schlatter et al. (1980)	Summer 1973 – spring 1974	La Dehesa, Chile	78.6	NA
Thompson and Anderson (1988)	Summers only, 1982–1983	Natrona Co., Goshen Co., WY, USA	88	5
Barrows 1989	Year-round, 1986–1988	Coachella Valley, CA, USA	73.7	NA
Schmutz et al. (1991)	Summer 1990	South-eastern Alberta, Canada	64	NA
Plumpton and Lutz (1993)	Summers only, 1990–1991	Adams Co., CO, USA	55.5	NA
Moulton et al. (2006)	Spring only, 2001–2002	South-western Idaho, USA	95	NA
Littles et al. (2007)	Winter only, 1999–2004	Southern coastal Texas, USA	98	29
Nabte et al. (2008)	Winter and summer, 2001–2002	Chubut, Argentina	77.2	5.6
Mrykalo et al. (2009)	Year-round, 2003-2004	Southwest FL, USA	97.5	NA
Trulio and Higgins (2012)	Year-round, 2005–2006	Santa Clara Co., CA, USA	94	30
Chandler et al. (2016)	Autumn 2010 – spring 2011	Southeast Farallon Island, CA, USA	66	1.5
Gonzalez Rojas et al. (2022)	Winter only, 2002–2005	Llano la Soledad, Nuevo Leon, Mexico	90	16

suggest a similar rodent community, but higher capture rates (9% trapping success); (Conroy 2005). This survey was similarly conducted in the spring, but years prior to our study (2005); interannual fluctuations in rodent populations prevent us from drawing strong conclusions from the comparison. However, rodent survey data from other regions of the burrowing owls' range lend additional support to the hypothesis that rodent prey was not abundant at our site (Moulton et al. 2006: 14.5% trapping success, Mills 2016: 33.6% trapping success).

As dietary generalists, burrowing owls often subsist on diets high in invertebrates (Moulton et al. 2006; Littles et al. 2007; Trulio and Higgins 2012). However, fledgling success and productivity may increase with the availability of vertebrate prey (Poulin et al. 2001, 2001; Ronan 2002). While our case study points to the possibility of preferred prey limitation at the site, our sample size was strongly limited by the small and transient nature of our focal burrowing owl population. Larger studies are necessary to understand the extent to which diet influences site fidelity in restoration sites, though such studies are made increasingly challenging by burrowing owl population declines.

Diet quality is one of many interacting ecological factors that determine habitat suitability for burrowing owls. We observed large raptors at the site, which may present competition for rodent prey as well as predation risks to burrowing owls. During the study period, we observed two instances of burrowing owl predation (one attempted, one successful) by red-tailed hawks (*Buteo jamaicensis* (Gmelin, 1788)) and one instance of a burrowing owl being repeatedly pursued by a peregrine falcon (*Falco peregrinus* Tunstall, 1771). The risk of predation and effects of interspecific competition may have additionally reduced the attractiveness of the restoration site for burrowing owls and contributed to their eventual abandonment of the site. Together with our diet findings, these observations emphasise the need to consider predator and prey populations when providing habitat for burrowing owls in restored habitats.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: KCCS, MMO, KS, AR, LS. Formal analysis: MMO. Investigation: KCCS, AR, KS, LS. Writing - original draft: MMO. Writing - review and editing: LS, MMO, KCCS.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Pellet contents raw data

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